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STUDIES IN ROOT-PARASITISM.

THE HAUSTORIUM OF SANTALUM album.

I.—EARLY STAGES, UP TO PENETRATION.

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THE HAUSTORIUM OF SANTALUM ALBUM.

1. EARLY STAGES, UP TO PENETRATION.

ATTENTION having been drawn to the sandal tree during recent years because of the occurrence of a serious and obscure disease in the plantations, it was thought worth while to make a careful study of the root system. Many points in the diagnosis of the disease seemed to indicate a root trouble.

There appeared to be considerable doubt as to the extent of the root-parasitism, long known to exist in the sandal, and many responsible officers openly expressed their doubt as to its existence. A study of this subject was therefore commenced. While much work has been done on the comparatively simple haustoria of various species of Thesium, it was somewhat surprising to find that the complex organs of attachment of so important an economic tree as the sandal had never been adequately described or figured. It was accordingly determined to prepare such a description.

A very large collection of the haustoria of sandal on different plants has been made for this purpose, the list of hosts being now considerably over one hundred in number. Most of these have been examined under the microscope, and the following paper is based on the results obtained.

While excavating these roots, my Botanical Assistant, Mr. C. Tadulingam, noted certain haustoria of a different appearance both as to colour and roughness from those of the sandal. With great labour these were traced to an entirely different plant, namely

Cansjera Rheedii. The occurrence of hemi-parasites among the *Olacineæ* was unknown to me, and this led to a more extended examination of the roots of jungle plants in the Madras Presidency. At first it was thought that this new feature would inevitably lead to the transference of *Cansjera* from the *Olacineæ* to the allied *Santalaceæ*, especially as there are other points connected with the structure of the ovary which would justify this change. But, on examining the roots of *Olax scandens*, a common creeping plant in the dry forests, and, so to speak, typical of the order, these were also found to be abundantly provided with haustoria freely attached to the roots of neighbouring plants. Recently I have come across a note by E. Heckel[1] on the occurrence of haustoria on the roots of seedlings on *Ximenia americana*, another of the *Olacineæ*, but these have not been observed in nature. A further study of the roots of *Olacineæ* is thus shown to be necessary, and may throw some light on the relative position of the different members of this rather heterogeneous order and on its relations to the *Santalaceæ*. This study will be prosecuted in all the species obtainable.

These facts are merely recorded here, and the description of these new haustoria, possessing many points of interest, will be reserved for another paper.

A visit to the hills of the Madras Presidency was taken advantage of to collect and examine the haustoria of *Osyris arborea*, another member of the *Santalaceæ*. The roots of this species and of *Thesium Wightianum* have been collected attached to many different hosts and they will receive attention later on.

It has been found unsafe to found the description of any of these haustoria upon the connections with only one or two foreign roots. This will abundantly appear in the course of the present paper. The collection of material, involving heavy manual labour in a tropical climate, is slow and fatiguing but, thus far, these various plants have been collected with attachments to some twenty hosts a piece. The number of hosts of the sandal, as already

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[1] Heckel, Sur le parasitisme du Ximenia americana. Comptes Rendus hebd. de l'Acad. des Sciences de Paris. T. cxxxi, 1900, pp. 764-5.

noted, greatly exceeds this number, and, for this reason, together with the importance of the tree from an economic point of view, the sandal haustoria have been selected for description first.

2. The true sandal, *Santalum album*, is a native of the Indian peninsula and is typically present in the native State of Mysore. From this region the bulk of the world's supply of sandal oil is obtained and the greater part of the Mysore forest revenue is derived from this source.

The distribution of the sandal is thus given in the Flora of British India. "Deccan Peninsula, from near Poona on the West, to Midnapur on the East (practically from Bombay to Calcutta) southwards, on dry hills, ascending to 3,000 feet; cultivated elsewhere." In the Madras Presidency sandal is chiefly found on these "dry hills," which may be regarded more or less as outliers of the Mysore plateau; and all regions in South India with elevation and climate at all similar to that between *Hunsur* and *Shimoga* in Mysore may be regarded as suitable for the natural growth of the sandal.

The plant is, however, found growing luxuriantly at many places at different elevations and with heavier rainfall. Sandal grows well in Madras city, and is found at various spots on the Malabar Coast, especially near Cannanore and Calicut. It is also found in the elevated plateau of the Wynaad, which is exposed to the full fury of the south-west monsoon, and it may be seen at Courtallam in Tinnevelly. But the plants growing in these localities, although very healthy, are destitute of the oil in the heartwood which makes the sandal tree so valuable. The typical region is one of small rainfall and an elevation of 2,000 to 4,000 feet. Here the growth is slow and the plants are frequently gnarled and meagre, but they are full of oil.

It is obvious from what follows that the plant is almost entirely dependent on the surrounding vegetation for its root nutriment. A useful indication of the limits of the true sandal region may be obtained from a study of the flora in its natural haunts, and such a study has been commenced.

3. The fact that *Santalum album* is a root parasite was first discovered by Scott in the Calcutta Botanic Gardens. Scott relates that he had noticed that when he transplanted sandal he was unsuccessful in getting them to grow unless a very large ball of earth was taken with them. And this was especially the case with old trees. From the analogy of *Thesium* and *Comandra*, both near allies, he thought of root-parasitism, and this he found to be the cause. He published the fact in the Journal of the Asiatic Society in 1871.[1] Solms Laubach translated Scott's paper in the Botanische Zeitung in 1874.[2]

It may be noted as a curious fact, that Scott considered the sandal as especially parasitic on palms, and he succeeded in obtaining connections with quite a number of species. It is doubtful, as will be seen from what follows, if true penetration was effected in all these cases. In the large collections more recently made in Mysore and Madras such connections with palms are exceedingly rare, and, from such observations as have been made, it would seem that the sandal has the greatest difficulty in penetrating monocotyledonous roots, especially those furnished with peripheral bands of sclerotic tissue such as are the rule in palms. This fact is in strict accordance with the scarcity of palms in the natural sandal tracts.

Solms Laubach appears to have studied the structure of sandal haustoria in specimens sent to him by Scott. In the few lines devoted to their anatomical description he finds no material difference from those of *Thesium*.

A brief illustrated account of the sandal haustorium was given in the "Indian Forester" for December 1904[3] and March 1905,[4] but, from the nature of that journal, these descriptions were more or less popular. In the present paper a somewhat fuller account is given of the early stages of the haustorium as far as penetration into

[1] Scott, Notes on Horticulture in Bengal, No. 2, Loranthaceæ, the mistletoe order, their germination and mode of attachment. Journal of the Agri-Horticultural Society of India, II, 2, Calcutta, 1871.

[2] Solms-Laubach, Botanische Zeitung, 1874, pp. 145-150.

[3] Barber, The Study of Sandal Seedlings, Indian Forester, December 1904.

[4] Barber, The Haustoria of Sandal Roots, Indian Forester, April 1905.

the host's tissues. A second paper will describe the structure of the mature haustorium, while an exhaustive study of the mutual influence of host and parasite is being likewise undertaken.

4. The haustorium of the sandal usually appears as a whitish conical mass, closely addressed to the roots of adjacent plants. At first cylindrical or hemispherical, it becomes elongated through the growth in length of the root attacked, in this respect contrasting with *Buckleya* whose haustorium has been recently described,[1] and where elongation takes place at right angles to the length of the root attacked, so as to keep pace with its secondary thickening. The shape of the mature haustorium may be generally described as a flattened cone or bell drawn out laterally on two sides. The area of attachment and the scar left behind by the haustorium are oval, and the contact surface is concave, fitting closely to the bark of the host (Pl. II, fig. 1).

The haustoria grow to a fairly large size. The largest met with in this investigation were, curiously enough, some found attached to old roots of sandal itself, whitish limpet-like bodies, reminding very strongly of the thorns with corky bases so characteristic of the bark of many Zanthoxylums. The usual dimensions of a fully developed haustorium may be stated as follows :—height 3—10 mm., longer diameter 2—12 mm., shorter diameter 2—8 mm. This difference in diameter in different directions is connected with internal structure, the organ being markedly bilateral, a fact which will be fully dealt with in considering the anatomy of the mature organ. Scott gives the diameter as from 3 to 8 lines (6—17 mm.), a size met with but unusual in South India.

Although the typical shape of a haustorium is that of a cone elongated along one diameter, many cases of irregularity occur. This is not surprising when we consider the conditions under which they are formed. Not only are they subject to the pressure exerted by the ordinary increase in thickness of the root attacked, but they

1 Kusano, Studies on the Parasitism of Buckleya quadriala, B. et H., a Santalaceous Parasite, and on the structure of its Haustorium. Journal of the College of Science, Imperial University, Tokyo, Japan, xvii. 10, 1902.

themselves, filled with plastic substances, and with thin-walled tissues rapidly growing, are firmly pressed against the particles of surrounding soil. This pressure causes them to fit the root of the host very closely, but their external form is frequently altered by unequal pressure due to differences in the soil. Among the curious forms met with may be mentioned a flat, lichen-like growth over the surface of the bark (Pl. I. fig. 6). Such a form is chiefly found when the root-attack is unsuccessful and the haustorium continues to grow. These extreme cases are rare, but it frequently happens, when entrance is difficult, that the haustorium is small and blister-like, as, for instance, in the various species of *Zizyphus*. All stages occur between this and the typical symmetrical cone described above.

A word may be said here on the so-called "terminal" haustoria. These have been discussed by Heinricher in *Lathræa* and, more recently, by Kusano in *Buckleya*. A case is here figured of such a haustorium of sandal on *Ficus religiosa* (Pl. I, fig. 7). From a careful study of many transitional cases and a consideration of the manner in which the haustoria are formed, it becomes evident that the general conclusion arrived at by these writers is correct, and that the terminal position is assumed owing to the atrophy of the part of the root beyond the point of attachment at an early stage of growth. A case illustrating this is shown in sandal (Pl. I, fig. 9), while particularly instructive examples are met with *Osyris arborea*, the atrophying part remaining attached as a minute tail long after it has lost its functions (Pl. I, fig. 8).

5. A sandal seedling, if carefully raised from sandy soil, is seen to have its roots covered with small white dots, the young lateral roots and haustoria. Many of these are found to be attached to the minute rootlets of grasses and other surrounding plants. To study this early stage of development of the root system it has, however, been found advantageous to grow the seedlings in pots, in pure sand. Those grown in earth and vegetable mould have usually abnormal, distorted and decayed roots.

The food contained in the seed is sufficient to keep the plant alive, healthy and green for a long period, and seedlings grown in

pure sand have been successfully reared for over a year. This long life without the aid of external nutriment is explained by the structure of the sandal seed and the early changes taking place in the seedling. The seed of the sandal is about the size of a pea, it is stored with albumen, in the centre of which the linear embryo lies with the radicle pointed upwards. On germination the radicle is protruded and immediately turns downwards. But the hypocotyl grows rapidly and soon forms a loop, the upper part of which rises above the surface of the ground. The seed rots and falls off, but not before the stores of food material have been transferred to the hypocotyl. This part of the seedling becomes greatly swollen in its lower half, and it is to this radish-like swelling of the hypocotyl that the growing seedling owes its existence until the roots are able to take on their natural function. The cotyledons have meanwhile broken off from the seed, the hypocotyl becomes erect, the petioles of the cotyledons remaining clearly visible as green stumps immediately above which the new leaves are rapidly unfolded. (Pl. I, fig. 2 *a* to *e*).

Haustoria are now developed in numbers upon the branching root system, demonstrating the fact that the presence of foreign rootlets is not necessary for their formation. Many of the haustoria are found attached to other sandal roots. This self-attachment is not uncommon in the seedlings of hemi-parasites. It has been noted in *Osyris arborea* and *Cansjera Rheedii*, and is especially characteristic of the root system of *Olax scandens*, while Heckel has marked it in the pot plants of *Ximenia americana* mentioned above. It has also been noted in seedlings of *Cuscuta*.

Most of the haustoria are however either free or attached to pebbles, bits of bark, etc., and, although their development does not proceed very far in these cases, a study of such simple forms will be found instructive.

The following passage regarding the formation of haustoria on the roots of sandal seedlings is quoted from my paper in the Indian Forester (December 1904), since that journal is not readily obtainable in botanical circles :—

"It has been noticed that when a rootlet commences to form haustoria, it usually does so in many places, so that rows of these are met with on certain

roots while others have none. Such roots are specially suited for the study of the early differences between true root branches and haustoria. As is well known, while the latter are formed from the external layers of the rootlet, the lateral roots are formed deep in its tissues and have to push their way out. The difference is at once seen on using a hand lens of moderate power. The young haustoria are conical, frequently flattened in the direction of the long axis of the root, with a broad base; while the rootlets are more or less cylindrical and pointed. The lateral roots are furthermore seen, one and all, to have at their base a minute collar of the tissue thrust aside in their outward progress, and after death this collar is left behind and forms a characteristic scar. This is clearly shown in the figures. Bearing this in mind, it is easy for anyone armed with a hand lens to study the development of haustoria and lateral roots on sandal seedlings. It is also worthy of note that in several rootlets examined dark fungus hyphæ were found in the cortex running parallel with the long axis of the root.

Seedlings grown in pure sand are light green in colour and, although perfectly formed, are evidently not well nourished. After a while the older roots appear to decay, their ends die, and the haustoria already formed become brown and hollow. New whiter roots are then developed higher up the hypocotyl to replace them.

Young plants in a mixture of vegetable mould and sand assume a darker colour and a more healthy appearance. There is little difference in the size of these seedlings and those grown in sand during the first six months, but, on pulling them out and examining the root system, this is seen to be very differently developed. Instead of the fine network of delicate rootlets, there is comparatively little branching. The roots are thicker, reminding one of those found in humus-loving plants, and there are fewer root hairs. These roots seem to be peculiarly subject to the attacks of insect enemies. In some pots every root end was found to have been destroyed as fast as it was formed, and this was apparently the work of a thin, active, long black ant. But even in the absence of insect enemies the roots were unhealthy, the branches quickly dying and leaving scars of characteristic appearance behind them all along the roots, and comparatively few healthy root ends were met with. There was a remarkable absence of haustoria on these roots, although they were very occasionally met with." (Pl. I, figs. 3—5).

This difference in the seedlings grown in pure sand and in vegetable mould is probably more marked in pot plants than in nature where the conditions of drainage are very different.

It should be noted that root-hairs are not absent from the sandal root system. But they are small and difficult to see without a lens. The haustoria in their earlier stages are covered with

root-hairs (Pl. I, figs. 5 and 5′), and, as will be seen later, the outer layers of tissue in these organs retain their power of growing out in a root-hair-like manner for a considerable period. When the outermost layer has become permanent, the cells beneath push their way through and behave in the same manner.

It is also to be noted that the formation of haustoria is more or less confined to the younger roots. The main roots of sandal, although clothed with large haustoria, probably take little part in the absorption of nutriment. Many of these haustoria are found on examination to be dead or at any rate moribund, while externally they appear to be full of vigour. I have thus been led to the conclusion that the actively absorbing haustoria are distributed on the root system in much the same manner as the younger roots with their root-hairs are in ordinary plants. The mature sandal roots show a curious incapacity for producing adventitious rootlets, and the same applies to their formation of haustoria. The root system may thus be divided, as in other plants, into the absorbing portion where multitudes of young haustoria are being formed, and the transmitting portion,—the older roots which no longer absorb, or at any rate do so in a limited degree. This subject will be dealt with when considering the structure of the mature sandal haustoria.

Various writers have suggested that the absence of root-hairs in quantity in these hemi-parasites indicates a corresponding degree of parasitism, and the rarity and extreme delicacy of the root-hairs of sandal thus incline one to suppose that its parasitism is very complete, a point of view that I have been led to adopt from many other facts.

6. The earliest stages in the development of the haustoria of the sandal and the other plants mentioned above will not be described here. The difficulties of collecting suitable material and of making serial sections in paraffin in Madras have hitherto prevented me from tracing the exact layers of the mother root from which the different parts of the haustorium arise, and the opinions expressed below as to their origin have been arrived at by the study of only such sections as are here figured.

The young haustorium first described (Pl. II, fig. 10) is more or less pear-shaped, the narrower part being that of attachment to the mother root. In sections the latter is seen cut across in various directions, in this case transversely. It is not to be supposed that the haustorial tissues have been derived from the development of the part of the mother root shown in this figure as it is not always easy to get a true median section through the whole organ. It will be seen later (Pl. II, fig. 11) that the endodermis opens out where the mother root joins the haustorium, and it seems probable that the upper, proximal part of the haustorium is formed, as in *Thesium* described by Leclerc du Sablon,[1] from tissues within the endodermal layer.

The body of the haustorium consists of thin-walled parenchyma. Towards the broader, distal end, the cells in the centre are seen to be less distinct, densely filled with protoplasm and rapidly dividing. In spirit specimens their colour is yellowish and their contents are turbid, as contrasting with the clear, white tissues around them containing large starch grains. This character affords a useful means of differentiation between meristematic cells and those that have become more or less permanent.

This yellowish indistinct area is the first stage in the development of the "nucleus" of the haustorium, the portions of the parenchyma on either side giving rise to the "cortex."

7. In the somewhat later stage next figured (Pl. II, fig. 11), the section has fortunately passed through the upper part of the haustorium in the median line. A double strand of vascular elements is seen to proceed from the mother root down the axis of the haustorium. This strand is accompanied by an endodermal layer on each side continuous with that of the mother root.

The meristematic cells at the distal end have increased in size and number and are now sharply marked off from the rest. In the case figured a small pebble has been encountered and the peripheral portions of the cortex are growing out so as to clasp it and hold

1 Leclerc du Sablon, Recherches sur les Organes d'Absorption des Plantes Parasites (Rhinanthacees et Santalacees). Annales des Sciences Naturelles, Bot., Ser. VII, vol. vi, pp. 90-117, 1887.

it fast. These "cortical folds" are a constant feature of the haustorium.

The latter may now be divided into the following parts. Passing along the axis, the nucleus is readily separable from the part above it. The latter, with its vascular strands, may be regarded as a region transitional between the mother root and the haustorium proper, and, from the study of many sections, it appears probable that it has been derived from that part of the mother root within the endodermis.

Laterally, on the other hand, the nucleus is equally readily distinguished from the cortex which, continuing to grow while the nucleus is obstructed by the pebble, has formed the two clasping folds. It will be seen later that the whole of the cortex is not thus produced, but that a portion of it remains undeveloped on both sides of the nucleus.

A narrow space appears to separate the haustorium from the surface of the pebble. This is filled with a felt-like mass of large cells (Pl. II, figs. 11 and 12). The origin of these cells is a little difficult to make out in the present section, but a more fortunate one through another small haustorium also fixed to a pebble, shows that it consists of hair-like outgrowths from the body of the haustorium (Pl. II, fig. 13). The outer layers have become compressed and form a dead protecting envelope to the living cells. These latter have however pierced the external dead cells and grown out after the manner of root-hairs.

8. The haustorium remains comparatively simple in structure if a living root is not encountered. Vascular elements are not formed in the nucleus, and those formed above it and connecting it with the mother root may be regarded as concerned not so much with the passage of fluids upwards towards the mother root as the transmission of materials to the nucleus and the parts around it for their further development. It will be interesting, when studying the early development of the haustorial tissues, to determine whether this upper portion is provided with sieve tubes as well as with endodermis. The later formed vascular strands of the haustorium proper are not thus provided.

But although the haustorial structure remains comparatively simple when these organs are attached to pebbles, certain changes are sometimes observable. The upper cells of the nucleus become collapsed by the pressure of the growing tissues below, and these collapsed cells form a dark band across the axis of the organ dividing the nucleus from the transitional region. Later on, with the growth in length of the parts, these dead or moribund tissues become torn and a series of lacunæ is formed in the upper part of the nucleus (Pl. III, fig. 14).

Meantime the whole of the lower, living cells are devoted to an effort at absorption and may be called, generally, the absorptive part of the haustorium. Wherever a foreign body is encountered the cells at the point of contact become glandular and excrete a yellowish mucilage-like substance charged with cyto-hydrolytic ferments. The cells of the haustorium also become absorbent, but it is not probable that the same cells perform both these functions. The structure of the secreting cells is completely broken down in this act, and traces of them can frequently be seen in the transparent mucilaginous mass. It appears to be the cells below them that take up the absorbing work just as we have seen the internal cells growing through the dead epidermal layers after the manner of root-hairs (Pl. II, figs. 12 and 13).

The haustorium figured (Pl. II, fig. 14) shows these points fairly well. The transverse band of collapsed cells at the top of the nucleus is not very clearly seen (*cf* however Pl. III, fig. 15 and Pl. IV, fig. 18) while the lacunar tissue is greatly developed. This haustorium was found firmly clasping a small pebble which was imbedded in the tissues and completely hidden from view. The glandular secretion can be seen as a dark mass in the angles of the two cortical folds. It may also be noticed in a similar position in the two succeeding figures.

9. When the foreign body encountered is soft, the absorbing tissue becomes greatly enlarged. Such for instance is the case in haustoria attached to the root-nodules of *Pithecolobium Saman.*

As an extreme example of this expansion a curious section is figured of a haustorium which has encountered the chrysalis of a

small Lepidopteron (Pl. III, figs. 15—17). The whole lower part has penetrated into it as a hemispherical mass of parenchymatous tissue, the epidermal cells secreting the yellow substance or protruding freely as root-hairs according to their position. Portions of the chitinous covering of the chrysalis are to be seen firmly held by the cortical folds, and these portions are imbedded in the secretion, presumably with the object of dissolving them.

10. The simple structure thus far described is generally the limit attained when the haustoria become attached to pebbles, bits of stick or bark or other unprofitable substances. But sometimes additional efforts at penetration are made. These efforts are much commoner when a living root of some resistance is attacked, and it will perhaps be better at once to proceed to the consideration of the latter case, as exhibiting the first stages in successful penetration. The efforts referred to give rise to the formation of "compound haustoria" or of a well-defined "gland," or of both together.

A compound haustorium may perhaps be best defined as one in which one or more nuclei are formed successively below the first which meantime loses its functions, while the inner layers of the cortex are prolonged to form new clasping folds. The appearance is that of two or more haustoria seated upon one another, and the evident object is to afford a new chance at penetration by the formation of new absorptive tissue and fresh clasping folds.

The absorptive tissue has not succeeded in its quest for nutriment. The inner parts of the cortex, that is to say, those parts which have not grown out to form the clasping folds, increase greatly by cell division. They push their way between the host and the existing folds, lifting these away from their point of contact (Pl. V, fig. 19). The nucleus shares in this development by becoming elongated. But this growth of the nucleus appears to take place chiefly in the lower part, the upper cells becoming empty and collapsed.

Such a compound haustorium is seen in Pl. III, fig. 15. The pairs of cortical folds are well shown, while the second nucleus is very clearly defined. The first-formed nucleus is limited above

by a transverse band of collapsed tissue. This band lies immediately below the dark strands of vascular tissue at the top of the figure, which mark the region of transition from the mother root. This character is shared by the lower nucleus which commences immediately below a similar set of vascular strands.

These repeated attempts at penetration are of especial frequency in the attacks on roots protected by concentric layers of sclerotic cells in the bark. Thus the haustoria on many leguminous roots are compound. In Pl. IV, fig. 18, a haustorium on *Pterocarpus indicus* is shown with four sets of cortical folds and four successive nuclei. An exceptional case has been noted where five separate attempts were made to penetrate a pebble, a fact which throws some doubt on the perfect adaptation of the haustoria for their work.

It may be noted in passing that Solms Laubach,[1] in his description of the haustoria of *Thesium*, divides them into two classes according as they attack monocotyledons or dicotyledons. In the former case the haustoria are compound while, in the latter, only one pair of folds is developed from the cortex. This difference is generally recognised as due to differences in the amount of resistance offered by the tissues of the host. The facts stated by Solms Laubach are probably to be explained as follows. Most monocotyledonous roots have peripheral sclerotic bands to protect their succulent inner tissues, whereas the roots of dicotyledons in temperate climates are not usually thus provided. The roots of *tropical* dicotyledons are, on the other hand, frequently armed by bands of hardened tissue in their bark and, wherever this is the case, compound haustoria are common. This explains their frequency in attacks on the Leguminosæ (Pl. IV, fig. 18, *scl*).

In the haustorium shown in Pl. IV, fig 18, the successive nuclear formations are clearly outlined. The upper part of each consists of cells devoid of contents, and there the tissues are clear and transparent. The oldest nucleus already shows a transverse band of collapsed cells. While, however, the axial cells of each nucleus cease dividing and become permanent, a layer on each side remains

1 Solms Laubach, Ueber den Bau und die Entwickelung der Ernährungs-organe parasitischer Phanerogamen. Jahrb. f. wiss. Bot. VI, p. 548, 1867-8.

living and capable of further development. At the top of the figure may be seen the vascular bundles cut across, which form the connection between the haustorium and the mother root. These bundles are continued round the sides of the nucleus and are thus continuous with the living cells on each side in which, later on, vascular elements are formed. There is thus left a passage by which nutriment can be readily passed from the mother root to the lowest part of the developing haustorium, and, if entrance is effected, for the reverse current of sap from the host to the parasite.

11. The effect of this long-continued attack in the case under examination is clearly seen in the tissues of the root where the haustorium touches it. The bark is discoloured and abraded and the cork has been entirely removed, small pieces being discoverable in the grasp of successive folds (*ck*). The layers of sclerotic cells, which have apparently borne the brunt of the attack, are discoloured also, but, thus far, are unbroken and offer a mechanical barrier to the glandular cells. The darker colour of the inner, cortical cells shows, however, that the influence of the secreting cells has passed beyond this barrier. This distant action of the haustorial cells through many layers of unruptured cells is not infrequently seen. From the appearances at the side of the haustorium, especially the broadening of the inner layers of the cortex, it seems probable that yet another pair of folds will be formed.

That the haustorium would ultimately succeed in reaching the xylem of the host's root in this case there can be little doubt. The haustorial tissues are still active and filled with protoplasm. In many cases examined this is not so. The disappearance of all contents from the tissues may indicate the change of the haustorium to a purely transmitting organ, as in the case of older roots in other plants, when a connection has been established between the vascular systems of host and parasite. But in some cases, as will be seen later, after such a connection has been established, the vascular strand decays at a certain point, and it is difficult to understand how it can continue to act as a channel for fluids. The organ is then probably moribund. On the other hand, if the cells become

permanent and empty without penetration, this probably indicates the final failure to obtain an entrance, fresh efforts being made lower down the mother root where the tissues are still in an active condition.

The exact part played in absorption by each haustorium is difficult to determine. In many ways, as already pointed out, the whole system of haustoria may be compared with that of the root-hairs of other plants. And the health or otherwise of the tissues of any given haustorium will probably depend, not only upon its age, but also on whether it is attached to the absorbing or transmitting part of the root system, a point which cannot be determined in the majority of cases because of the difficulty of laying bare the roots. The haustoria of *Buckleya quadrialà*, as has been pointed out by Kusano, are provided with a well-marked secondary thickening, live for many years and undergo remarkable changes as age advances, but there are reasons for limiting the period during which the haustoria of sandal are effective.

12. But, besides the healthiness of the tissues in the haustorium figured, there is another reason for assuming that its efforts at penetration would ultimately be successful. This is the presence of a well-defined *gland*. The frequent occurrence of glands is a most interesting feature of the sandal haustoria. They have also been met with in *Cansjera* and *Olax* and their differences noted. Those in *Olax* are the most complicated, while those in *Santalum* and *Cansjera* are almost indentical and comparatively simple.

I have not at present met with a description of glands in haustoria. Solms Laubach observed something of the kind in *Thesium*, as may be seen from the following quotation[1]:—"Häufig findet sich in der Längsachse dieses Gewebes die Andeutung einer Linie, die besonders dicht oberhalb des Beginnes der Saugfortsatzes deutlich, und hier bisweilen sogar zu einer schmalen Lücke im Gewebe erweitert ist. Diese Linie wird immer beiderseits durch etwas convergirende und über das normale Mass vergrösserte

[1] Solms Laubach, l.c., Jahrb. f. wiss. Bot. vi, 545.

Zellen begrenzt : wo sie als Lücke im Gewebe auftritt, ragen die anstossende Zellen papillen-artig in sie vor, und ist in derartigen Papillen der in einem Netz von Protoplasmasträngen aufgehängte Zellkern ganz besonders deutlich zu erkennen."

The structure of the gland in *Santalum* agrees in general with the above description, and it seems probable that glands will be found in *Thesium* as well as in the other haustoria mentioned in this paper.

13. The gland makes its first appearance in the lower part of the nuclear mass, near the surface of contact with the root of the host. It forms a median strand of turbid cells whose colour in spirit specimens is of a denser yellow than the rest, this being, as already pointed out, a rough indication of protoplasmic contents.

Such a stage is shown in Pl. V, fig. 19, where a haustorium is attempting the almost impossible task of penetrating the root of *Ochlandra Rheedii*. The roots of this bamboo have a heavy sclerotic armature (Pl. V, fig. 20) and, although a number of attached haustoria have been examined, not one has been met with that has succeeded in penetration, nor indeed was there evidence of its exerting any influence on the outer layers of the root attacked. The median, darker band of cells is the first stage in the development of the gland. The section is further interesting as showing a double haustorium in formation. On one side the growing cortex has already formed a second fold and the first is lifted away from the root, on the other side this stage has not been reached, but the growing edge of the second fold is clearly seen pushing its way downwards and outwards.

In thin sections the structure of the cells in this early stage may be studied. They are seen to be densely filled with granular protoplasm and have distinct nuclei with large nucleoli (Pl. V, fig. 21). Several of the cells are seen to be on the point of division. The neighbouring cells of the " nucleus," while also protoplasmic, have large central vacuoles.

14. The cells of the gland rapidly arrange themselves in two rows in the middle line. These become the actual secreting cells.

A cleft appears between them, commencing at the point furthest removed from the root of the host and gradually extending in its direction. The gland thus frequently appears to be wider at the top and diminishes downwards until it ends in a narrow channel resembling a duct.

Such a stage is seen in Pl. V, fig. 18, as well as Pl. V, fig. 22, which latter represents a section through a young haustorium fixed upon another sandal root as host. The limits of the nucleus are clearly defined, as also is the path to be subsequently taken by the vascular strands connecting it with the mother root.

Stretching across the open part or lumen of the gland may be seen delicate transparent cell-walls which meet in the middle line. A careful examination under higher power shows that the secreting cells have greatly increased in length and that the "opening" of the gland is due to this. The lower part of each cell is seen to be filled with a peculiarly dense substance, while the upper part, *i.e*, that towards the centre of the gland, is perfectly clear. This is well seen in the present case (Pl. V, fig. 23). The cells of the gland, although apparently widely separated, are still in organic connection, as is seen by the dovetailing of their walls in the middle line.

The length of the lower protoplasmic part of the cell varies a good deal, but is usually small in comparison with the rest. In Pl. V, fig. 24, it is greater, and the gland cavity is full of a granular mucilaginous substance evidently arising from the secreting cells. This hides the upper part of the cells, including their walls. It seems possible that this represents an earlier stage in secretion, and that the granular base of the cell gradually diminishes as fresh mucilage is poured out.

At a later stage of development the gland cavity widens still more and the gland cells are torn apart. The ends of these cells are now either ruptured or rounded and protruding into the cavity (Pl. V, figs. 25 and 26). The gland cavity is seen to be filled with curved rods of granular substance whose diameter agrees very closely with that of the secreting cells. A fortunate part of the section shows that the rods do actually arise from individual cells (Pl. V, fig. 26) the ends of which are open.

In the two figures last referred to a series of curved lines are seen throughout the upper, clear parts of the cells. It is natural to assume that these lines represent the limits of successive secretions. This stage is not of frequent occurrence in the gland sections examined. It would appear that the secreted substance, formed at intervals, passes freely through the cell walls and leaves a limiting membrane behind it as a sort of skeleton. The space above the last curved wall is filled with granular secretion.

The base of the secreting cells is filled with a very dense uniform substance, presumably protoplasm. In its appearance and structure it appears to agree very closely with that described by Gardiner in *Dionaea*[1] and *Drosera*[2] cells at the end of secretion. The protoplasm in these, from being granular, becomes dense and uniform, the upper part of the cell is filled with a large vacuole, the secretion is poured out in drops which "taking up water are forced outwards and take on a rod-like appearance." The same clearing of the protoplasm is described by Brown and Morris[3] in the cells of the epithelium of the scutellum of the barley at an early stage in germination. Attention may be drawn in passing to the presence, recently demonstrated, of glands in the epithelial layers of the scutellum of *Zea Mais*, as the function of these in many ways resembles that of the haustorium under description.

From the nature of the case it has not been possible to observe the effect of stimuli on the structure of the gland cells in *Santalum*. In figure 24 the protoplasm is more granular, and the suggestion has already been made that this represents an earlier stage in secretion. In older stages the protoplasm of the gland cells is easily distinguishable from that of the surrounding cells by its highly refractive character, and in spirit specimens it assumes a bright golden colour. A closer examination of the basal protoplasmic layer in the specimens last figured shows that there is a series of

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1 Gardiner, on the Changes in the Gland Cells of Dionæa muscipula during Secretion. Proc. Roy. Soc., xxxvi, pp. 180-1, 1883-4.

2 Gardiner, on the Phenomena accompanying Stimulation of the Gland Cells in the Tendrils of Drosera dichotoma. Proc. Roy. Soc., xxxix, p. 229.

3 Green, on Vegetable Ferments. Annals of Botany, vii, pp. 123, et seq., 1893.

papillæ at its upper end, which project into the cell cavity, and probably this structure has something to do with the secreting function (Pl. V, fig. 27).

15. The cells of the young haustorium arrange themselves in certain definite lines which indicate the direction in which growth is taking place and cell divisions are most frequent. In the earlier stages these lines of growth are, generally, at right angles to the surface of contact between the haustorium and its host, and this is especially seen when the root is large and the haustorium forms a flattened cushion, but in older stages and in smaller roots, where the clasping folds grow round the circumference, the lines become curved downward towards the median line, and this arrangement is especially so when the mass of cells forming the nucleus becomes distinct (Pl. II, fig. 11). The lines of growth are then curved round the developing nucleus and the parts immediately above it. In thin sections, indeed, the rows of cells are seen to be continuous right up to the median line occupied by the gland. Such is the case in Pl. V, fig. 22 and Pl. VI, fig. 28.

This simple arrangement of the cells in definite curves is however about to undergo considerable alteration, especially if penetration has been effected The growing of the cortical folds round the root's circumference causes certain changes. The cells at the edge of the fold become arranged as in a vegetative apex, converging to the edge, and as a result of the extension of this part subsidiary curves appear on each side between the growing edges and the median line (Pl. V, fig. 22). The nuclear mass increases in size, and the cells between it and the surface of contact are squeezed flat and ultimately disappear. At the same time an important change is taking place in the cells of the nucleus itself at each side. A succession of rapid divisions takes place there parallel to the nuclear surface, that is to say at right angles to the former lines of growth. The result of these divisions is the formation of a narrow band of elongated cells which, while obscuring the former lines of growth, furnish the procambial strands from which the vascular elements are derived on each side. Such a stage is shown in Pl. VI, fig. 28

which, however, is slightly diagrammatic (see description of figures at the end.)

16. The cortex meantime undergoes a change of some importance in the development of the haustorium, and a thorough understanding of what takes place here is necessary for that of much that follows. Speaking generally, the older, upper and outer parts of the cortex have now played their part and become changed to permanent tissue. Divisions cease and the cells become emptied of their contents, these layers now being merely protective of those within. But the cells of the inner cortex, that is to say, that part which is in contact with the nucleus, remain capable of growth and division for some time longer. That this is necessary will at once be evident when it is considered that the median parts of the haustorium must rapidly elongate as soon as an entrance is effected, and, for the central parts thus to grow in length while the outer remain permanent would inevitably lead to serious rupturing of the tissues. The cortex thus becomes separated into two regions, the outer cells becoming permanent and empty, while the inner are charged with contents, especially large starch grains, and presumably remain turgid. These two parts of the cortex are divided from one another by a well-marked " separation layer."

By the continued increase in the size of the nucleus considerable pressure is exerted outwards on each side. This pressure is not along the lines of growth which are curved upwards, but directly outwards on each side, and its presence is indicated by a line of collapsed cells at the junction of the inner and outer parts of the cortex. This division of the cortex and the first formation the " collapsed layers " are clearly seen in Pl. V, fig. 22. Collapsed layers are formed later on at various other parts of the haustorium, and in all cases serve as an index of the direction of pressure at a particular stage of growth and the death of the cells concerned. The collapsed layers on either side here mentioned are the chief ones, and are present in all haustoria built on this type. such as those of *Thesium*, *Buckleya*, *Cansjera*, *Olax*, *Osyris*. They are always formed at the junction of living turgid cells

and such as have ceased to grow, become permanent and lost their contents.

17. There are several factors which combine to assist the haustorium in penetrating the root of the host. In the first place, considerable pressure is exerted. This must obviously be the case when we consider that both the haustorium and the root attacked are increasing in bulk while firmly imbedded in the soil. Signs of this pressure are seen in the collapsed layers in the haustorium itself, in the crushing of the cells between the developing nucleus and the surface of contact, in the transverse band at the top of the nucleus, in the not infrequent alteration in shape of the attacked root which is sometimes much flattened, and in the burrowing action of the clasping folds (Pl. V, fig. 22). Lastly, the cells of the root attacked are not infrequently seen to be crushed as the process from the haustorium enters, and even large, thick-walled vessels are completely flattened to the occlusion of their lumen.

But the cells of the haustorium have, as we shall see in studying the mature organ, also the power of secreting a cyto-hydrolytic ferment capable of dissolving the cell walls. This ferment appears to be formed whenever the haustorial cells come into contact with foreign bodies. And where the external cells of the haustorium have become crushed and dead, the layers beneath appear to have the power of taking on their function, sometimes with the result that the external layers themselves are dissolved. This secreting power, possessed in a certain degree by all the living cells of the haustorium, is especially developed where a gland is present. The substance secreted has the power to pass through the cells of both haustorium and host, as is evidenced by the alteration in the cell walls at a considerable depth in the tissues attacked, directly opposite to the surface of contact. Examples of this are by no means uncommon, but their consideration will be deferred until the mutual influence of host and haustorium on one another are considered and the different means of defence and attack adopted by different species of plants are discussed.

Whatever means are adopted for penetration, the intruding process, which may be termed the "sucker," shows itself keenly

alive to the advantage of proceeding along the path of least resistance, and curious cases have been noted where the lobes of the sucker have been diverted from the direct path to the vascular system and have wandered aimlessly along between sclerotic strands of tissue in the bark. For the present it will suffice to discuss two interesting cases of penetration that have been noted, the one with a gland and the other without.

18. In the hundreds of sections of haustoria examined, very few have been met with in which the intruding process is in the act of passing through the cortex. Either no entrance has been effected, with or without the presence of a gland, or actual contact has taken place between the absorbent cells and those of the woody cylinder. This rare occurrence of the entering stage seems to indicate that the growth of the sucker through the cortex is extremely rapid. For some time the tissues of the haustorium, especially in the neighbourhood of the nucleus, have been rapidly dividing and form a dense mass of small protoplasmic cells opposite the point of contact. When a breach has been made in the outer protective layers of the host's root, a tongue-like process is thrown forward by the mere elongation of these cells (Pl. VI, fig. 29).

But here, as elsewhere along the entire line of development, there are differences in the attacks on different species of plants. Thus it has been found that half-entered suckers are frequently to be met with in the species of *Zizyphus* examined. The cortex of the root in this genus is provided with a series of bands of thick-walled cells with softer tissues between. The tongue-like process has been pushed as far as one or other of these bands, and a halt has been made before a renewed effort at penetration has commenced. Many of the haustoria appear to have made no further attempt, and the cells in these are empty and moribund. I have figured a fortunate example of a penetrating stage in a sandal attacking *Asparagus racemosus*, in this case without the preliminary formation of a gland (Pl. VI, fig. 29). The presence or absence of a gland cannot be predicted in any given case. In other haustoria on the same plant glands were found, and no general rule can be laid down for their formation.

The tongue-like process of the sucker has pierced the cortex but has not yet penetrated the inner sclerotic bands. Although contracted, the cells appear to be healthy and are full of protoplasm.

19. It has already been noted that the mode of development of the haustorium varies a good deal with the kind of root attacked. In some species, for instance, almost every section shows an interesting stage of development, while in others every root cut has few points worth noting. The sections through *Kigelia pinnata*, *Thespesia populnea* and *Pterolobium indicum* have proved to be exceptionally interesting. In these three species the gland is usually present and is widely open below. In the first two of these, and in no others as yet examined, actual penetration of the cortex, with the aid of the gland, has been observed. In both cases the open gland is seen to be imbedded in the tissues of the cortex and there are no apparent mechanical cells in the way. The glandular cells are seen to be pouring out masses of mucilaginous substance. The cells of the nucleus are seen in the process of elongation, those nearest the apex of the tongue being the longest and those further away shorter according to distance (Pl. VI, fig. 32 *a-d*). The cells, both of the haustorium and of the cortex of the host, at the point of contact are partially dissolved.

In *Thespesia populnea* (Pl. VI, fig. 30) the gland is still fairly intact, and a fissure has been made reaching right through the cortex to the woody cylinder of the root. In *Kigelia pinnata* (Pl. VII, fig. 31) the gland is nearly obliterated and most of the secretion seems to arise from the neighbouring cells of the sucker. The latter section is further interesting as showing the changes taking place both in the nucleus and the cortex of the haustorium during penetration. The collapsed layers of the cortex are very distinctly seen as well as the change of direction in the curves of the growth in the inner and outer cortex. In the nucleus the peripheral bands of procambium are keeping pace with the rest in their growth and form a convenient boundary between the nucleus and the inner cortex.

As has been stated, these two cases of actual penetration are the only ones hitherto met with in the presence of a gland. It

cannot therefore be assumed that the opening of the gland is universal, although it seems probable that it is usual. In *Pterolobium indicum* the opening of the gland seems to be the rule, and this whether the sucker has succeeded in entering or not. The opening of the gland before the sucker has penetrated has not been elsewhere observed, but from its frequency in *Pterolobium* it would seem that there is something peculiar in the relations between that plant and sandal. Most of the haustoria on *Pterolobium*, whether reaching the wood or not, early lose their vitality and many are already dead (Pl. VII, fig. 34).

It is easy to see in a haustorium which has already reached the xylem of the host whether a gland has been present or not. The upper part of the gland remains for a considerable time as a median split in contact with the xylem although its cells are emptied of all contents.

When the haustorium has effected an entrance and the sucker has reached the central woody cylinder, it divides into two lobes, one on either side, which grow along the cambial line. This is the line of least resistance in the majority of cases. The cambium is completely destroyed at the surface of contact, and the edges of the lobes of the sucker are provided with glandular cells actively dissolving the tissues in front of them. The action of these cells and the very various means adopted by different species and genera for obstructing their further growth cannot be considered here. Suffice it to say that the capacity for resistance differs greatly, and also that the growth of the sucker into or around the woody cylinder is very different in different species. Advantage is taken of broad medullary rays to pass directly inwards or, in softer roots, the sucker bores its way irregularly into the xylem. This it appears to do in monocotyledonous roots but, as already stated, cases of successful penetration have been rarely met with in monocotyledons.

Certain strands in the elongated tissues of the sucker become vascular, and these become continuous with the lateral procambial bands of the nucleus. Connection is thus effected with the tissues of the xylem of the host. An outer layer of the nuclear procambium

remains meristematic and forms a well-marked cambium from which new vessels and medullary rays are formed. And thus in older roots broad bands of vascular tissue are met with. But here again the influence of the host is seen, and secondary thickening of the wood of the sucker is very much greater in some hosts than in others. The remaining parts of the haustorium become permanent and the cells lose their contents.

The study of the tissues of a mature haustorium is, however, complicated by the fact that we have to deal with a markedly bilateral organ. Sections have to be made in three directions before the character of the different elements can be understood. A second paper will deal with the structure of the mature haustorium.

Botanical Laboratory, Madras,
October 1905.

DESCRIPTION OF FIGURES.

Plate I.

Fig. 1. A root of *Lantana Camara* with sandal haustoria attached (natural size).

Plate II.

Fig. 2. Germination of the sandal. Note the persistent cotyledon stalks *cc*, and the swollen hypocotyl (natural size).

Fig. 3. A part of the root of a sandal seedling grown in pure sand, natural size and magnified. The lateral roots *r* and the haustoria *h* are clearly distinguishable.

Fig. 4. A young lateral root much magnified.

Fig. 5. A young haustorium also magnified. 5′. The end of the same showing root-hairs.

Fig. 6. Flat, lichen-like haustorium (natural size).

Fig. 7. Old, "terminal" haustorium on a root of *Ficus religiosa*. In the same figure is shown the scar left by another, dead haustorium (natural size)

Fig. 8. Old, "terminal" haustorium of *Osyris arborea*. The part of the *Osyris* root beyond the point of attachment is seen as a delicate black tail. Note the spiral curvature of the roots in these two cases.

Fig. 9. An old sandal haustorium showing the atrophy of the root beyond the point of attachment. This will become a "terminal" haustorium if it lives long enough.

Plate II.

Fig. 10. Section through a very young haustorium, *m* mother root, *h* haustorium. The nucleus *n* is being developed at the distal end as a mass of cells with denser contents.

Fig. 11. Section through an older stage. The haustorium is grasping a pebble *p*, *m* mother root, *tr* transitional region between the mother root and the haustorium proper. In this region a vascular strand is seen proceeding from the mother root to the nucleus. Note *e* the endodermis, *n* the nucleus, *cc* the cortex, *f-f* the cortical folds. Note also the lines of growth.

Fig. 12. The portion of the last haustorium between the nucleus and the pebble, magnified ; *n* nucleus, *rh* the felt-like mass of hairs protruding from it.

Fig. 13. A section through the same region in another haustorium attached to a pebble. The point of origin of the hairs is seen. They arise from the sub-epidermal layers and push their way through the outer, dead layers.

PLATE III.

Fig. 14. An older haustorium of simpler structure. This had a pebble imbedded in its tissues, which had to be removed before cutting the sections. Note the vascular cylinder of the mother root *m*, the transitional region with vessels and endodermis *tr*, the lacunar portion of the nucleus *l*, the absorptive portion of the nucleus *ab*, the cortical folds *f-f*, the glandular secretion in the angles of the folds *gl*, and the collapsed layers *cl*, *cl*.

Fig. 15. A small double haustorium attached to an empty chrysalis. The absorptive region *ab* of the nucleus is swollen to a hemispherical mass of parenchyma, part of which is pouring out secretion and part growing in a root-hair-like manner. The other letters are as in figures 14 and 18.

Fig. 16. The angle of a cortical fold in figure 15 magnified. A piece of the chitinous coat *ch* of the chrysalis is surrounded by secretion *gl* poured out by the outer cells of the nucleus.

Fig. 17. The median portion of the nucleus in figure 15 magnified to show the out-growth of the cells as root-hairs *rh*.

PLATE IV.

Fig. 18. A compound haustorium fixed to a root of *Pterolobium indicum*. There are four pairs of cortical folds *f-f*^{3} in whose angles pieces of the cork *ck* of the host are imbedded in glandular secretion. The successive nuclei are seen at *n* to *n*^{3}. On their outer borders layers of turbid cells *pr* have been formed, which unite the vascular tissues of the mother root to the youngest nucleus. Vessels are already being formed in the upper part of these procambial strands. A gland *gl* is forming in the median line of the youngest nucleus. The root attacked is abraded and darkened at the point of contact. *ck* cork, *scl* sclerotic cells, *camb* cambium, *xy* wood, *cl* collapsed layers.

PLATE V.

Figs. 19, 20. A sandal haustorium on *Ochlandra Rheedii* with a gland in its earliest stage *gl*. The haustorium is becoming double, two cortical folds having already been formed on one side. In figure 20 the sclerotic armature of the *Ochlandra* root is seen magnified further.

Fig. 21. The young gland of figure 19 under higher power. The median cells are densely filled with granular protoplasm and have no vacuoles. Some are actively dividing and the nuclei and nucleoli of these cells are very distinct.

Fig. 22. A small haustorium fixed to another sandal root, a case of self-parasitism. There is a well-developed gland in the middle line. Note especially

the curved lines of growth, the commencement of the collapsed layers, and the cavity and "duct" portions of the gland. The clasping cortical folds have exerted considerable pressure upon the young root attacked and have altered its shape.

Fig. 23. A portion of the gland in the last figure under higher power. The cells of the limiting epithelial layer are quite distinct from those below them in shape and contents. The lumen of the gland is seen to be permeated by delicate lines, dove-tailing in the middle line. These are the upper ends of the epithelial cells, filled with clear, mucilage-like secretion.

Fig. 24. A younger gland in which the epithelial cells have more granular contents. The cells are unusually elongated, and the granular substance in the lumen of the gland renders the cell-walls indistinct.

Figs. 25, 26, 27. Epithelial cells of glands highly magnified. The lower part of each glandular cell is filled with a dark, non-granular, highly refractive mass. The upper part is transparent and shows a series of curved, parallel lines, the limiting membranes of successive secretions. The space outside the cells, the lumen of the widely opened gland, is filled with rods of granular secretion which have been emitted by the epithelial cells. In figure 27 the basal protoplasmic mass of the cell is seen to have small processes projecting into the upper part of the cell.

Plate VI.

Fig. 28. The "duct" portion of a gland greatly enlarged and slightly diagrammatic, taken from a haustorium fixed on a root of *Tecoma stans*. The epithelial cells of the gland *ep* are seen on the left of the figure. They are arranged in two lines, and the space between them is continuous with the lumen of the gland. On the right are seen the starch-filled cells of the inner cortex *c*. Adjoining these are the outer cells of the nucleus. The latter have, by parallel divisions, formed a layer of elongated, narrow cells from which the procambial strands will be derived *pr*. In them the transverse divisions will cease, and they will become greatly elongated in comparison with the cells around. (See also 32 e.)

Fig. 29. A sandal haustorium in the act of penetrating the root of *Asparagus racemosus*. There is no gland. The distal part of the haustorium has been thrust forward into the cleft in the *Asparagus* root, but has been arrested by the inner sclerotic band outside the woody cylinder. The tongue-like sucker has shrunk. This is perhaps due to the action of the spirit, but possibly the haustorial end is moribund owing to failure in penetration. The transitional region, the upper boundary of the nucleus, the procambial strands, the collapsed layers and the elongation of the cells of the nucleus, are clearly shown.

Fig. 30. A portion of a sandal haustorium sucker entering a root of *Thespesia populnea*. The gland is present and is opened at the base. The epithelial cells

are clearly seen, as is also the turbid mucilage-like secretion exuded from them. The cortex of the host is split to the cambium and the cells lining this split are darkened and disorganised.

Plates VI & VII.

Figs. 31, 32. A sandal haustorium in the act of entering a root of *Kigelia pinnata*. There are many interesting points in this section. The lines of growth have become broken but are still traceable. The collapsed layers separate the cortex into two very distinct parts, and are thus not infrequently termed "separation layers." The cells of the inner cortex are remarkably large and regular in their arrangement. They are filled with large starch grains. Those cells of the inner cortex, however, which are contiguous with the elongating nucleus, have lost their starchy contents and are being drawn out as the sucker penetrates. The procambial strands of the nucleus are distinctly seen (see 32 e). The cells of the nucleus have become elongated, especially in the lower, terminal part of the sucker. Figs. 32, a to d, show these cells at different parts, from the top of the nucleus to the end of the sucker.

Plate VII.

Fig. 33. This figure shows the end of sucker of figure 32 enlarged. The great elongation of the nuclear cells is well shown, as also the epithelial lining of the opened gland. The space between the sucker cells and the tissues of the host is seen to be permeated by indistinct lines, the cell-walls of the secreting cells. It is seen that the outer cells of the sucker are all secreting, this action not being confined to the epithelial cells of the gland. The effect of the secretion is seen on the disorganised cell-walls of the cortex of the host's root.

Fig. 34. A haustorium of sandal attacking a root of *Pterolobium indicum*. Although no entrance has been effected, and merely the outer corky layers of the root have been torn off, the gland is widely opened, and the axial portion of the haustorium has become thrust away from the root attacked.

PLATE I.

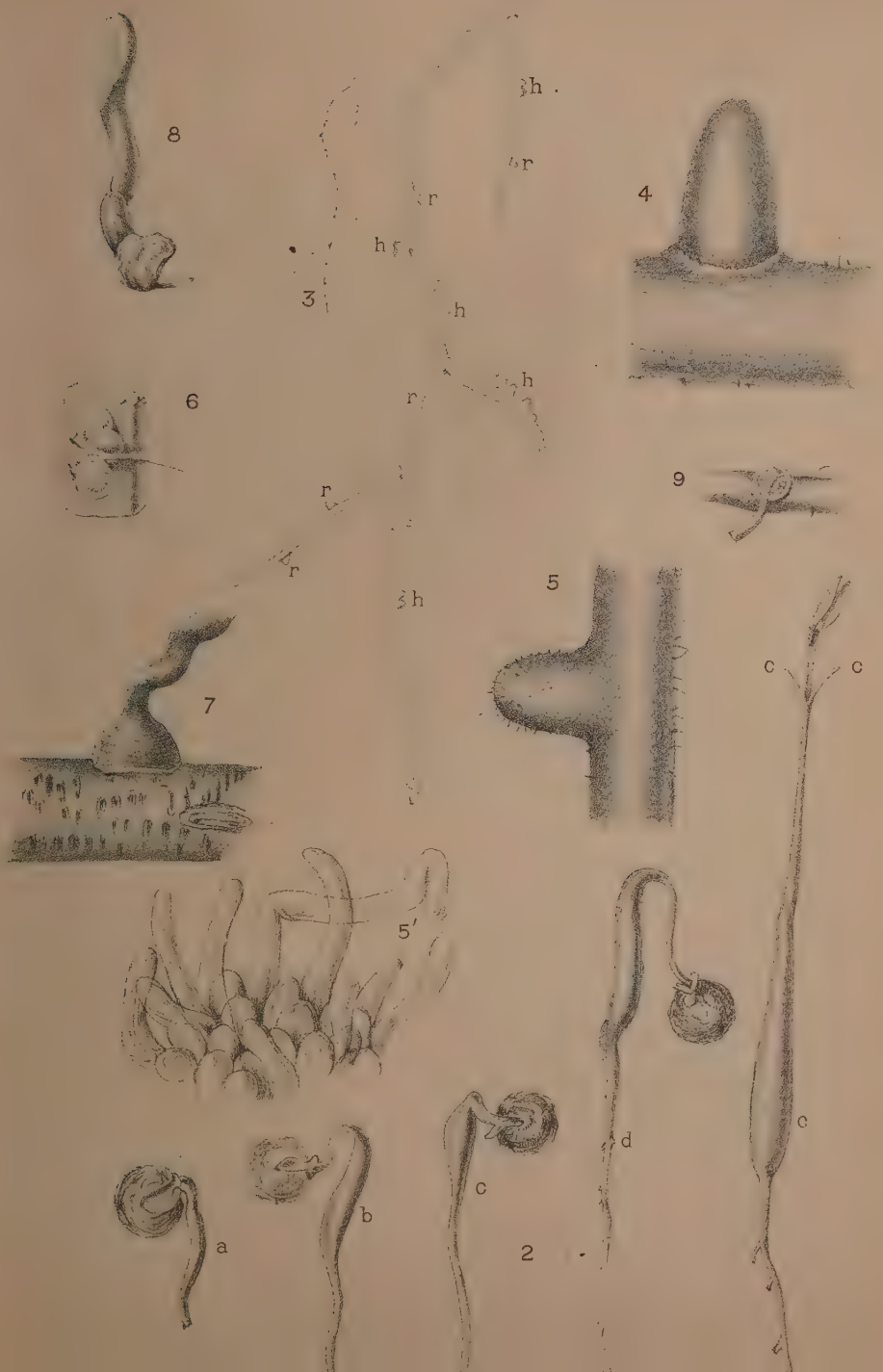
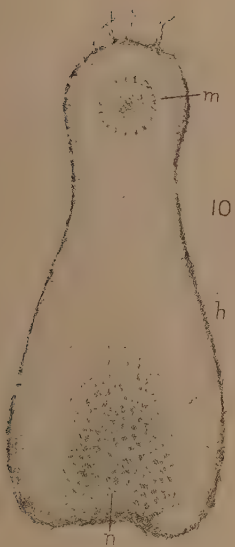


PLATE II.



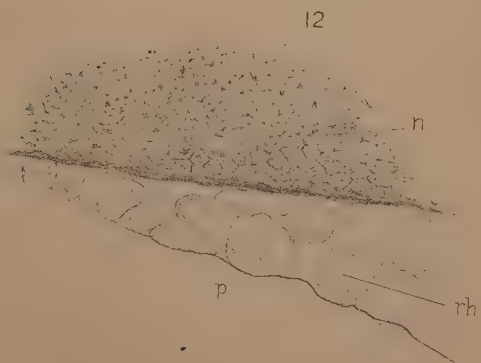
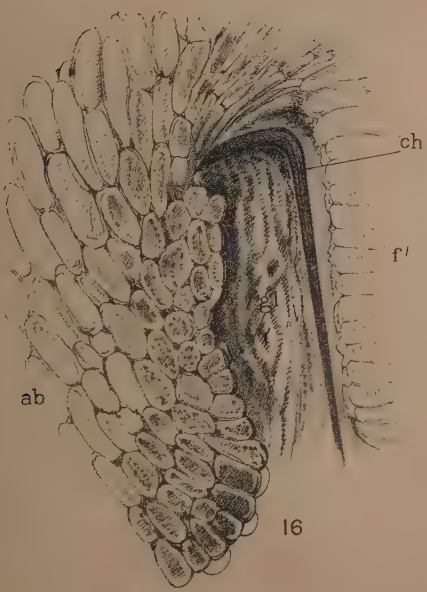
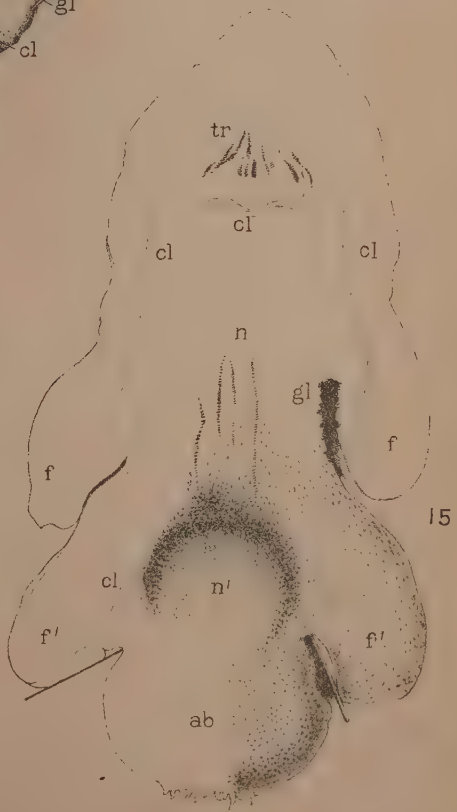


PLATE III.

14
m
tr
l
cl
gl
ab
gl
cl
f
f

17
rh


ch
f'
ab
16


tr
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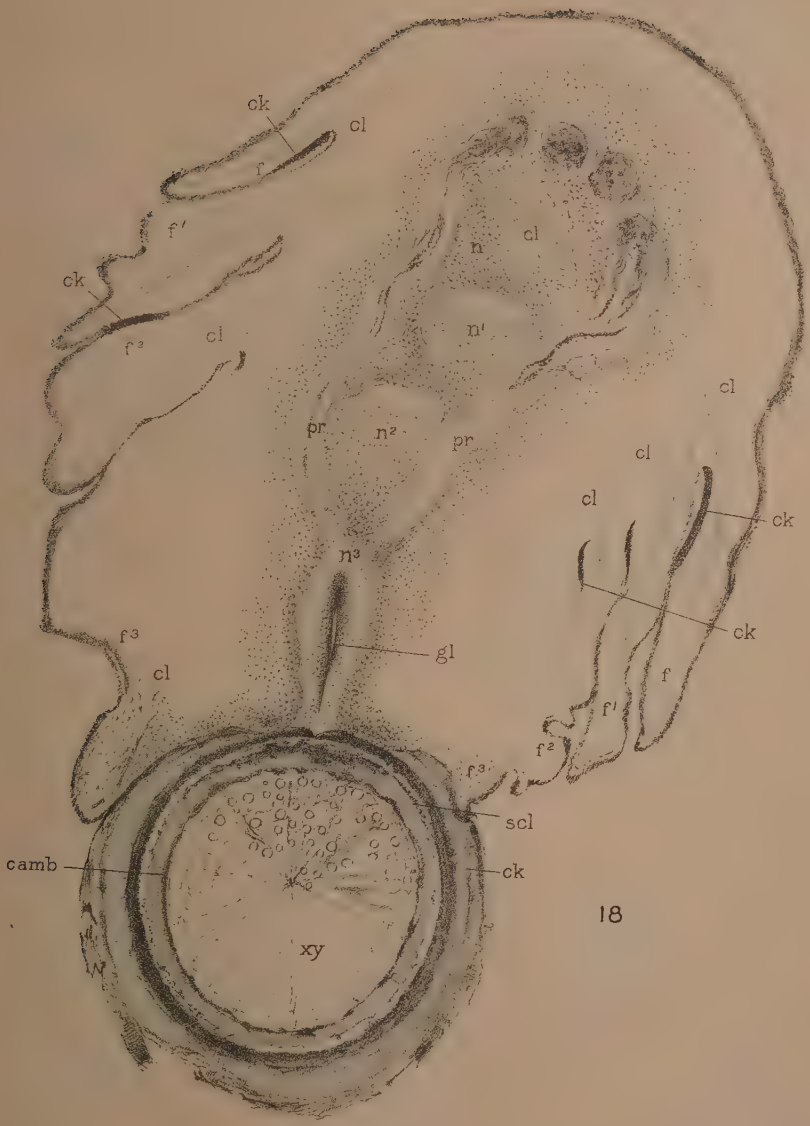
cl
cl
n
gl
f
f
15
cl
n'
f'
f'
ab

PLATE IV.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f
f'
ck
f²
cl
n
cl
n'
pr
n²
pr
cl
cl
cl
ck
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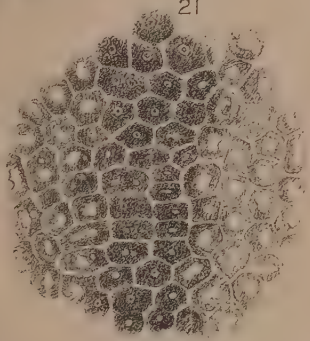
ck
f³
cl
gl
f
f'
f²
f³
scl
camb
ck
xy
18

PLATE V.



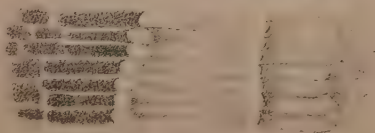
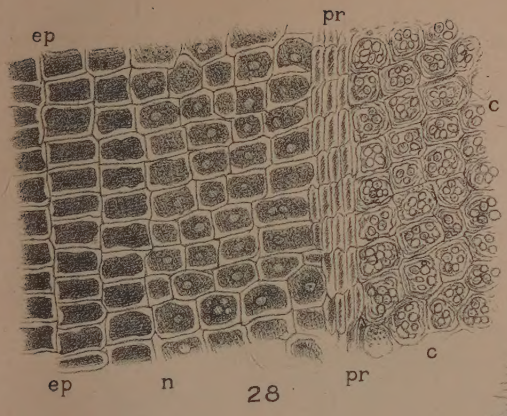
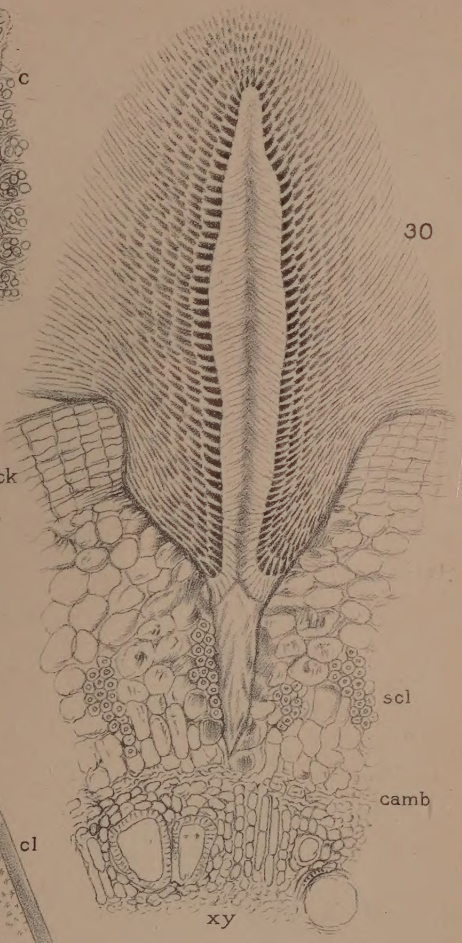
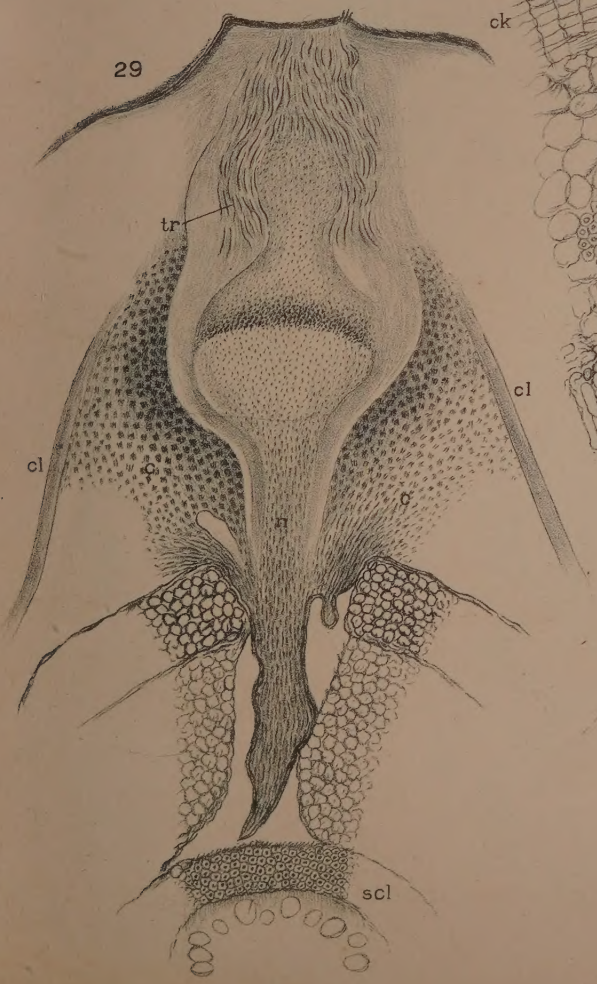


PLATE VI.







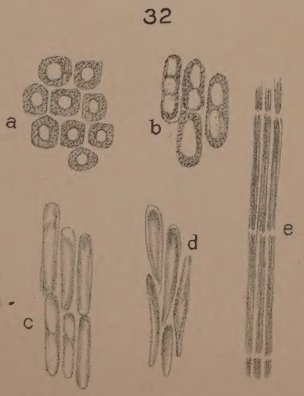


PLATE VII.